2002. The Journal of Arachnology 30:47–56

CYTOGENETIC HETEROGENEITY IN COMMON HAPLOGYNE SPIDERS FROM ARGENTINA (ARACHNIDA, ARANEAE)

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ABSTRACT. The spermatogenesis of four species of haplogyne spiders from Argentina is analyzed. *Dysdera crocota* (Dysderidae) (n = 5 + X0) has holokinetic chromosomes, achiasmatic male meiosis and a post-reductional division of the sex chromosome. *Ariadna boesenbergii* (Segestriidae) (n = 4 + X0) also possesses holokinetic chromosomes, but meiosis is chiasmatic and the X chromosome divides pre-reductionally. *Kukulcania hibernalis* (Filistatidae) (n = 11 + X_1X_20) and *Scytodes globula* (Scytodidae) (n = 6 + X0) have metacentric and submetacentric chromosomes, chiasmatic meiosis and the sex chromosomes divide pre-reductionally. *Kukulcania hibernalis* possesses a bimodal karyotype and a particular chromatin coiling during prophase I, while *Scytodes globula* has striking proximal localization of chiasmata. These results show that Haplogynae present high cytogenetic heterogeneity: species with holokinetic chromosomes as well as species with monocentric chromosomes (metacentric and submetacentric), and species with low diploid numbers, achiasmatic meiosis and proximal chiasma localization.

Keywords: Haplogyne, cytogenetics, meiosis

Phylogenetic knowledge of the higher systematics of Araneae has greatly increased recently (Coddington & Levi 1991; Griswold et al. 1999), and relationships have been analyzed largely on the basis of morphological characters. Cladistic evidence suggests that classical Haplogynae were originally defined on the basis of a plesiomorphy: absence of fertilization ducts in females, a character considered as primitive. Nevertheless, Filistatidae, Dysderoidea and the remaining "scytodoids" are considered a monophyletic group (Coddington 1990a, 1990b; Coddington & Levi 1991; Platnick et al. 1991; Griswold et al. 1999). This work is aimed to provide cytogenetic data that will be useful for assessing

Table 1.—Karyotype characteristics and collecting locality of the haplogyne species cytogenetically analyzed.

Species	2n	n (male)	Locality	References
Dysderidae				
Dysdera crocota C.L.Koch 1839	11	5+X0	Argentina	**This work**
D. crocota		?+X0	Uruguay	Benavente & Wettstein 1977,1980; Benavente 1982 (*sub D. crocata*)
D. magna Keyserling 1877	9	4+X0	Uruguay	Díaz & Sáez, 1966a, 1966b
Filistatidae				
Kukulcania hibernalis (Hentz 1842)	24	$11+X_1X_20$	Argentina	**This work**
Pholcidae				
Crossopriza lyoni (Blackwell 1867)	24	$11+X_1X_20$	India	Sharma et al. 1959
Pholcus crypticolens Bösenberg & Strand 1906	24	$11+X_1X_20$	Japan	Suzuki 1954
P. phalangioides (Fuesslin 1775)	24	$11+X_1X_20$	Argentina	Rodríguez Gil et al. 2000
Physocyclus californicus Chamberlin & Gertsch 1929	15	7+X0	U.S.A.	Cokendolpher 1989
P. enaulus Crosby 1926	15	7+X0	U.S.A.	Cokendolpher 1989
Physocyclus sp.	15	7+X0	U.S.A.	Cokendolpher 1989
Spermophora senoculata (Dugès 1836)		$?+X_1X_20$	U.S.A.	Painter 1914 (*sub Spermaphora meridionalis* Hentz 1841) (sic!)
Scytodidae				
Scytodes globula Nicolet 1849	13	6+X0	Argentina	**This work**
S. globula	13	6+X0	Uruguay	Díaz & Sáez 1966a, 1966b (*sub S. maculata* Holmberg 1876)
Segestriidae				
Ariadna boesenbergii Keyserling 1877	9	4+X0	Argentina	**This work**
A. mollis (Holmberg 1876)	9	4+X0	Uruguay	Díaz & Sáez 1966a, 1966b
A. lateralis Karsch 1881	7	3+X0	Japan	Suzuki 1954
? *Segestria florentina* (Rossi 1790)		$?+X_1X_20$	Uruguay	Benavente & Wettstein 1980; Benavente 1982 (possibly misidentified. Most probably *S. ruficeps*)
S. ruficeps Guerin 1832	14	$6+X_1X_20$	Uruguay	Díaz & Sáez 1966a
S. senoculata Linne 1758	14	$6+X_1X_20$	Japan	Suzuki 1954
Sicariidae				
Loxosceles laeta (Nicolet 1849)	23	$10+X_1X_2Y$	Perú	Silva 1988
L. reclusa Gertsch & Mulaik 1940	18	$8+X_1X_20$	U.S.A.	Tugmon et al. 1990
? *L. rufescens* (Dufour 1820)	20		Brazil	Beçak & Beçak 1960 (possibly misidentified, see Silva 1988, Tugmon et al. 1990)
? *L. rufipes* (Lucas 1834)	20	$9+X_1X_20$	Uruguay	Beçak & Beçak 1960; Díaz & Sáez 1966a (possibly misidentified, see Silva 1988, Tugmon et al. 1990)

relationships among basal members of the Araneomorphae.

Araneae comprises about 108 families and more than 3000 described genera (Platnick 2001). Cytogenetic data in the order, based on about 100 genera and 300 species, reveal the presence of acrocentric and telocentric chromosomes, a male diploid number between 7 and 94, with most species having 2n = 22, 24 or 28, a multiple sex chromosome determining system $X_1X_20/X_1X_1X_2X_2$ (85% of the species) and chiasmatic meiosis (Suzuki 1954; White 1973; Maddison 1982, 1996; Gowan 1985; Tugmon et al. 1990; Scioscia 1997). Of these species, only 6% belong to the Haplogynae, and they show particular heterogeneous cytogenetic features that differ from the general characteristics of the order. Cytogenetic data in haplogyne spiders are summarized in Table 1.

Within Haplogynae the genera *Dysdera* Latreille 1804 (Dysderidae), *Segestria* Latreille 1804 and *Ariadna* Savigni & Audouin 1825 (Segestriidae) display holokinetic chromo-

somes (chromosomes with diffuse kinetic activity due to the presence of non-localized centromeres) (Rieger et al. 1991), and achiasmatic meiosis (Appels et al. 1998) has been suggested in *Dysdera* and *Segestria* (Díaz & Sáez 1966a, 1966b; Benavente & Wettstein 1977, 1980; Benavente 1982). The presence of holokinetic chromosomes has been reported in a few invertebrate groups and in some plants, which indicates its polyphyletic origin (White 1973; Grant 1989; Greilhuber 1995; Vanzela et al. 1998). Although entire orders possess this chromosomal type (e.g., Odonata, Heteroptera, Homoptera, Phthiraptera) (Ueshima 1979; Mola 1995; Spence & Blackman 1998; Tombesi et al. 1999), within the Arachnida, holokinetic chromosomes are present in buthid scorpions (Shanahan 1989) and mites of the suborder Prostigmata (Oliver 1977), besides the spider genera already mentioned.

Achiasmatic meiosis has been reported in different invertebrate groups and, among plants, only in the *Fritillaria japonica* group (Liliaceae) (John 1990). This type of meiosis has originated independently, and appears to be a secondarily acquired feature from a chiasmatic meiosis, since in Diptera, mantids and enchytroids achiasmatic meiosis is found in the more advanced forms (John 1990; Appels et al. 1998). In Arachnida, achiasmatic meiosis has been also described in scorpions of the family Buthidae (Shanahan 1989).

In the present work, four species belonging to the spider group Haplogynae have been cytogenetically analyzed: *Ariadna boesenbergii* Keyserling 1877 (Segestriidae), *Dysdera crocota* C. L. Koch 1839 (Dysderidae), *Kukulcania hibernalis* (Hentz 1842) (Filistatidae) and *Scytodes globula* Nicolet 1849 (Scytodidae).

METHODS

The following specimens from Argentina were analyzed (number of individuals and collecting locality are indicated):

Dysdera crocota: 9 individuals (4 males, 2 immatures and 3 females). Ciudad Autónoma de Buenos Aires and Río Luján (Buenos Aires Province).

Ariadna boesenbergii: 27 individuals (7 males, 2 subadult males, 10 immatures and 8 females). Ciudad Autónoma de Buenos Aires.

Kukulcania hibernalis: 27 individuals (22 males, 1 subadult male, 3 immatures and 1 subadult female). Ciudad Autónoma de Buenos Aires, Rojas, Martín García Island Natural Preserve and Buenos Aires city surroundings (Buenos Aires Province); and Departamento Capital (Tucumán Province).

Scytodes globula: 13 individuals (5 males, 6 subadult males, and 2 immatures). Martín García Island Natural Preserve, Río Luján and Buenos Aires city surroundings (Buenos Aires Province).

Voucher specimens are deposited in the Museo Argentino de Ciencias Naturales (MACN) Arachnology collection.

The specimens of *A. boesenbergii* were mainly collected from *Tipuana tipus* trees, while the remaining specimens were collected from houses and neighboring constructions. Living specimens were bred at the Arachnology Department of the MACN.

Individuals were fixed in 3:1 (absolute ethanol : glacial acetic acid); gonads were dissected out and slides were performed by the squash method in iron propionic haematoxylin (Núñez 1968).

RESULTS

Mitotic and meiotic cells suitable for cytogenetic analysis were only observed in 4 males of *Dysdera crocota*; 1 male, 2 subadult males and 2 immatures of *Ariadna boesenbergii*; 6 males and 1 subadult male of *Kukulcania hibernalis*; and 4 males, 4 subadult males and 1 immature of *Scytodes globula*.

Dysdera crocota: this species is 2n = 11, n = 5 + X0 (male). In spermatogonial mitoses three larger chromosomes are detected (one autosomal pair and the X chromosome), and the lack of a primary constriction is evident (holokinetic chromosomes) (Figs. 1A, B). At meiotic prophase I the sex chromosome is positively heteropycnotic. After pachytene no typical diplotene or diakinesis stages are observed, due to the absence of chiasmata. Bivalents decondense later originating a homogeneous chromatin mass with the X still positively heteropycnotic (Fig. 1C). The chromatin mass then divides into 2 or 3 blocks (Figs. 1D, E). Bivalents continue separating except for the two smaller which remain associated (Fig. 1F). At prometaphase I the X chromosome turns isopycnotic, and among

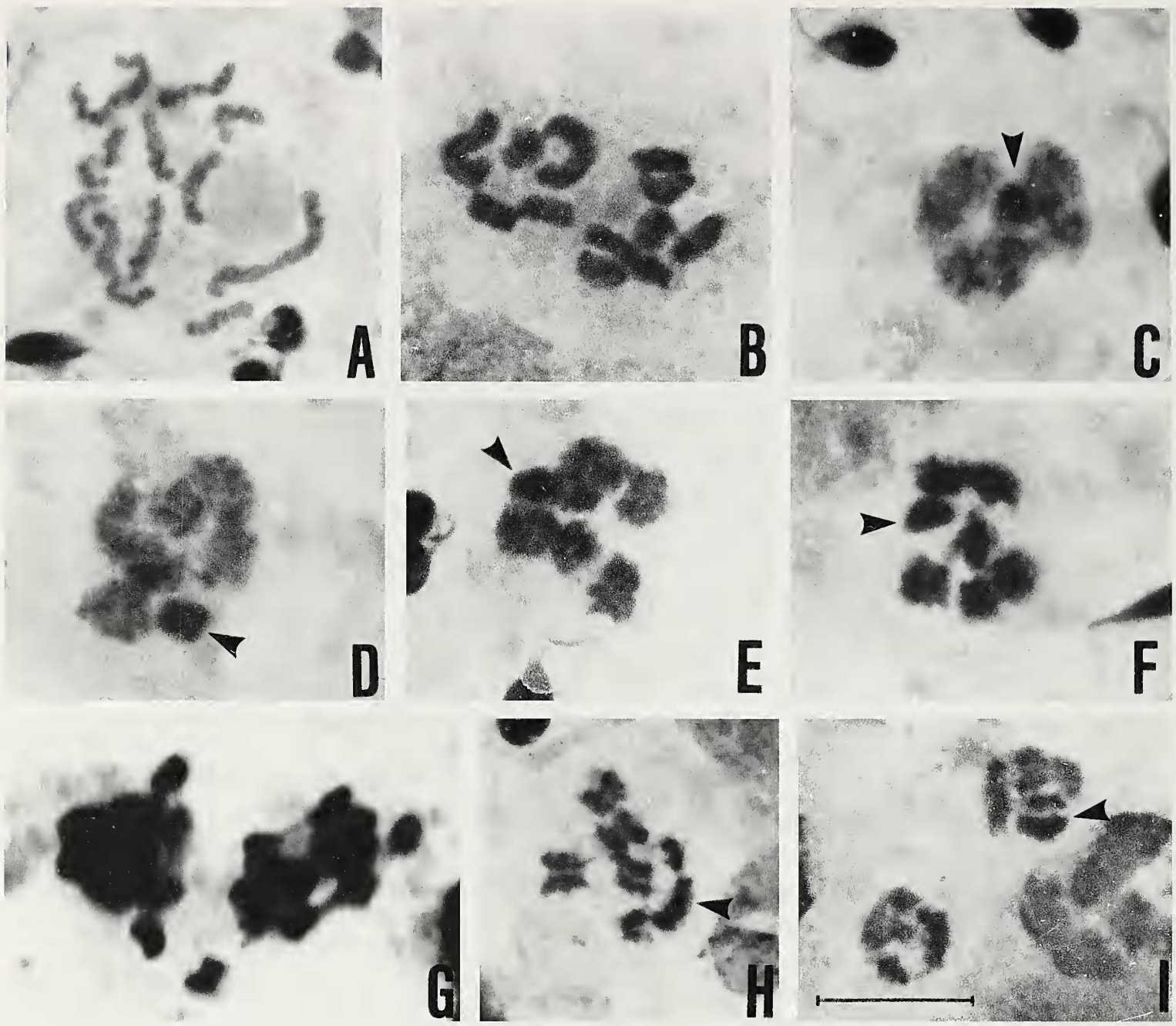

Figure 1.—*Dysdera crocota* (2n = 11, n = 5 + X0) A) Mitotic prophase. B) Mitotic prometaphase. C-E) Prophase I. F) Prometaphase I. G) Anaphase I. H) Metaphase II; one chromosome has already separated its chromatids. I) Telophase II. Scale = 10 μm. Arrowheads point to the X chromosome.

autosomal bivalents one larger and four of similar size are recognized. At anaphase I the sex chromosome divides precociously and equationally, separating sister chromatids (Fig. 1G). At metaphase II the autosomes lie with their long axis parallel to the equatorial plane while the X lies at the periphery (Fig. 1H). The sex chromosome divides reductionally at anaphase II, originating telophase II nuclei with and without the sex chromosome (Fig. 1I).

Ariadna boesenbergii: this species is 2n = 9, n = 4 + X0 (male). At spermatogonial prophase it is evident that chromosomes are holokinetic, and five larger chromosomes are distinguished (two autosomal pairs and the X chromosome) (Figs. 2A, B). At meiotic prophase the sex chromosome is slightly positively heteropycnotic. At diplotene two large and two small bivalents are observed, while the X chromosome is even a little smaller than the latter. At diakinesis the largest bivalents always possess two chiasmata while the smaller ones generally have only one chiasma. Mean chiasma frequency is 7.02 (Fig. 2C), and occasionally three chiasmata are formed in large bivalents. At metaphase I the sex chromosome is out of plate (Fig. 2D) and at anaphase I it migrates undivided to one pole, lagging behind the autosomes (pre-reductional division) (Fig. 2E). At metaphase II the chromosomes lie with their long axis parallel to the equatorial plane (Figs. 2F, G). The X chromosome divides equationally and precociously at anaphase II (Fig. 2H).

Kukulcania hibernalis: this species is 2n =

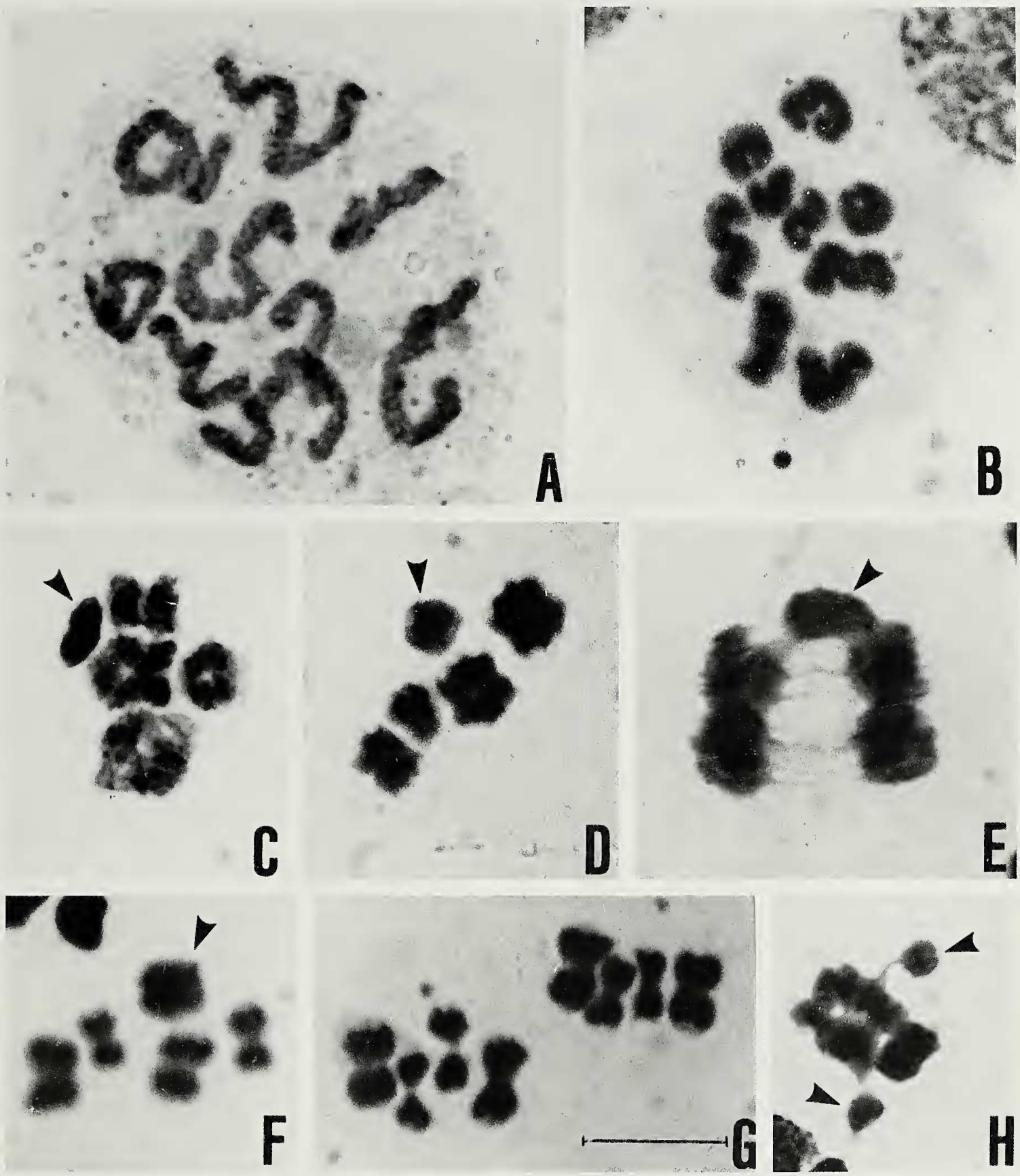

Figure 2.—*Ariadna boesenbergii* (2n = 9, n = 4 + X0). A) Mitotic prophase. B) Mitotic prometaphase. C) Diakinesis with three ring bivalents. D) Metaphase I. E) Anaphase I. F) Metaphase II with X chromosome. G) Metaphases II without X chromosome. H) Anaphase II. Scale = 10 μm. Arrowheads point to the X chromosome.

24, n = 11 + X_1X_20 (male), with metacentric and submetacentric chromosomes. At spermatogonial prometaphases four extremely large autosomes are distinguished, while the sex chromosomes cannot be identified. At pachytene, bivalents arrange in a bouquet, and no positively heteropycnotic body is observed (Fig. 3A). Bivalents then decondense completely and enter a diffuse stage in which it is difficult to individualize them. During this long diffuse stage the sex chromosomes are condensed, being positively heteropycnotic and intimately associated (Fig. 3B). One of the large autosomal bivalents does not decondense completely, remaining slightly positively heteropycnotic and usually showing a ring

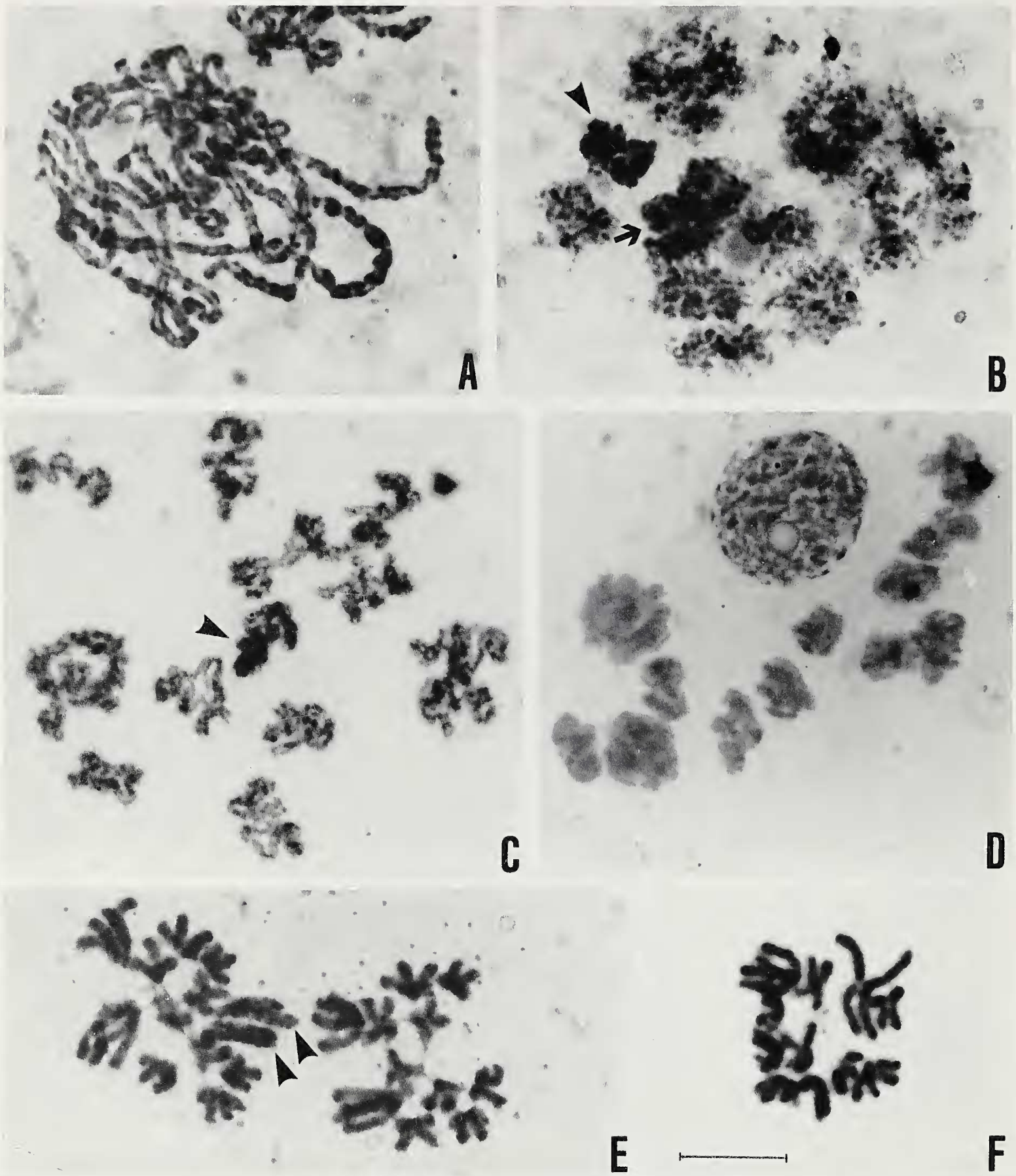

Figure 3.—*Kukulcania hibernalis* (2n = 24, n = 11 + X_1X_20) A) Pachytene. B) Diffuse stage; arrow points to the less decondensed bivalent. C) Diplotene. D) Prometaphase I. E) Telophase I. F) Metaphase II without X chromosomes. Scale = 10 μm. Arrowheads point to the X chromosome.

shape. The other large bivalent is frequently observed associated to a nucleolus. At diakinesis bivalents recondense adopting a particular morphology, and the sex chromosomes continue positively heteropycnotic (Fig. 3C). Bivalents present one chiasma except one of the larger ones that generally presents two chiasmata. At prometaphase I bivalents and the sex chromosomes are isopycnotic (Fig. 3D). At anaphase I the sex chromosomes (X_1X_2) migrate together to the same pole (pre-reductional division) (Fig. 3E); it is clear that the sex chromosomes are large and unequal in size. This species presents two kinds of meta-

phase II, with and without sex chromosomes (11 autosomes + X_1X_2 and 11 autosomes, Fig. 3F). At the second meiotic division the sex chromosomes divide equationally.

Scytodes globula: this species is 2n = 13, n = 6 + X0 (male), with metacentric and submetacentric autosomes of similar size, and a submetacentric sex chromosome. At early prophase I the X chromosome is positively heteropycnotic (Fig. 4A). At diplotene and diakinesis it is evident that all bivalents present one chiasma next to the centromere (Fig. 4B, C). A few cells with one bivalent with two chiasmata have been observed; when they have two chiasmata, one is proximal and the other distal (Fig. 4B). At metaphase I the sex chromosome lies outside the equatorial plate (Fig. 4D), and at anaphase I it migrates undivided to one pole lagging behind the autosomes (pre-reductional division) (Fig. 4E). Metaphases II with (Fig. 4F) and without the sex chromosome are observed. At anaphase II the X chromosome divides equationally and synchronously with the autosomes. Telophase II nuclei with and without sex chromosomes are observed (Fig. 4G). At both anaphase I and anaphase II the sex chromosome is thinner and larger than the autosomes, and it is slightly negatively heteropycnotic.

DISCUSSION

Cytogenetic studies on haplogyne spiders reveal marked differences from the general characteristics of the order: the presence of holokinetic chromosomes and achiasmatic meiosis have been reported in some species of Dysderidae and Segestriidae; and in species with monocentric chromosomes, the metacentric and submetacentric morphology is frequent. The diploid chromosome numbers of these species are the lowest or among the lowest known for the order (2n = 7 to 2n = 24).

Previous reports on *Dysdera* agree with our results utilizing Argentinean individuals of *Dysdera crocota* with reference to the holokinetic nature of its chromosomes, the post-reductional division of the sex chromosome, the achiasmatic meiosis and the low chromosome number (Table 1) (Díaz & Sáez 1966a, 1966b; Benavente & Wettstein 1977, 1980; Benavente 1982). However, karyotypic data on *D. crocota* were absent (Benavente & Wettstein 1977, 1980; Benavente 1982).

Within the Segestriidae, the genera *Ariadna* and *Segestria* have been studied (Table 1). Díaz & Sáez (1966b) described in *Ariadna mollis* (Holmberg 1876) a haploid number of n = 4 + X0 with holokinetic chromosomes, and Suzuki (1954) described n = 3 + X0 in *A. lateralis* Karsch 1881. *Ariadna boesenbergii* (n = 4 + X0) presents the same sex chromosome determining system and also a low diploid number. In this species, as well as in *A. lateralis* (Suzuki 1954) the sex chromosome migrates late and pre-reductionally, and these observations bring us to suggest that the "lagging bivalent" described by Díaz & Sáez (1966b) in *A. mollis* at anaphase I is a misinterpretation of the lagging X chromosome. *Segestria ruficeps* and *S. senoculata* also present a low chromosome number, but a multiple sex chromosome determining system ($X_1X_20/X_1X_1X_2X_2$) (Table 1). In *S. florentina* (most probably *S. ruficeps*) Benavente & Wettstein (1980) described the presence of holokinetic chromosomes, achiasmatic meiosis and pre-reduction of the sex chromosomes.

In summary, Segestriidae and Dysderidae share two cytogenetic traits uncommon within the order, and even in the animal kingdom: holokinetic chromosomes and achiasmatic male meiosis. The fact that the only three genera cytogenetically analyzed until now have holokinetic chromosomes should suggest that this characteristic could have had a common origin; on the other hand, the absence of chiasmata in *Dysdera* and *Segestria* could have originated independently, since it is not a common feature to both families.

Kukulcania hibernalis and *Scytodes globula* are the only species of Filistatidae and Scytodidae cytogenetically analyzed. The chromosome number of *Kukulcania hibernalis* is one of the most frequent in the order, and its sex determining mechanism is typical of Araneae, although it differs since it has metacentric and submetacentric chromosomes, and a bimodal karyotype. On the other hand, *Scytodes globula* also displays characteristics uncommon to the order: a low diploid number, metacentric and submetacentric chromosomes, and a proximal chiasma localization, which causes the particular bivalent morphology. Díaz & Sáez (1966a, 1966b) studied males of *Scytodes globula* from Uruguay, and they found the same chromosome number and similar meiotic characteristics to those described here.

It is noteworthy that in the species here an-

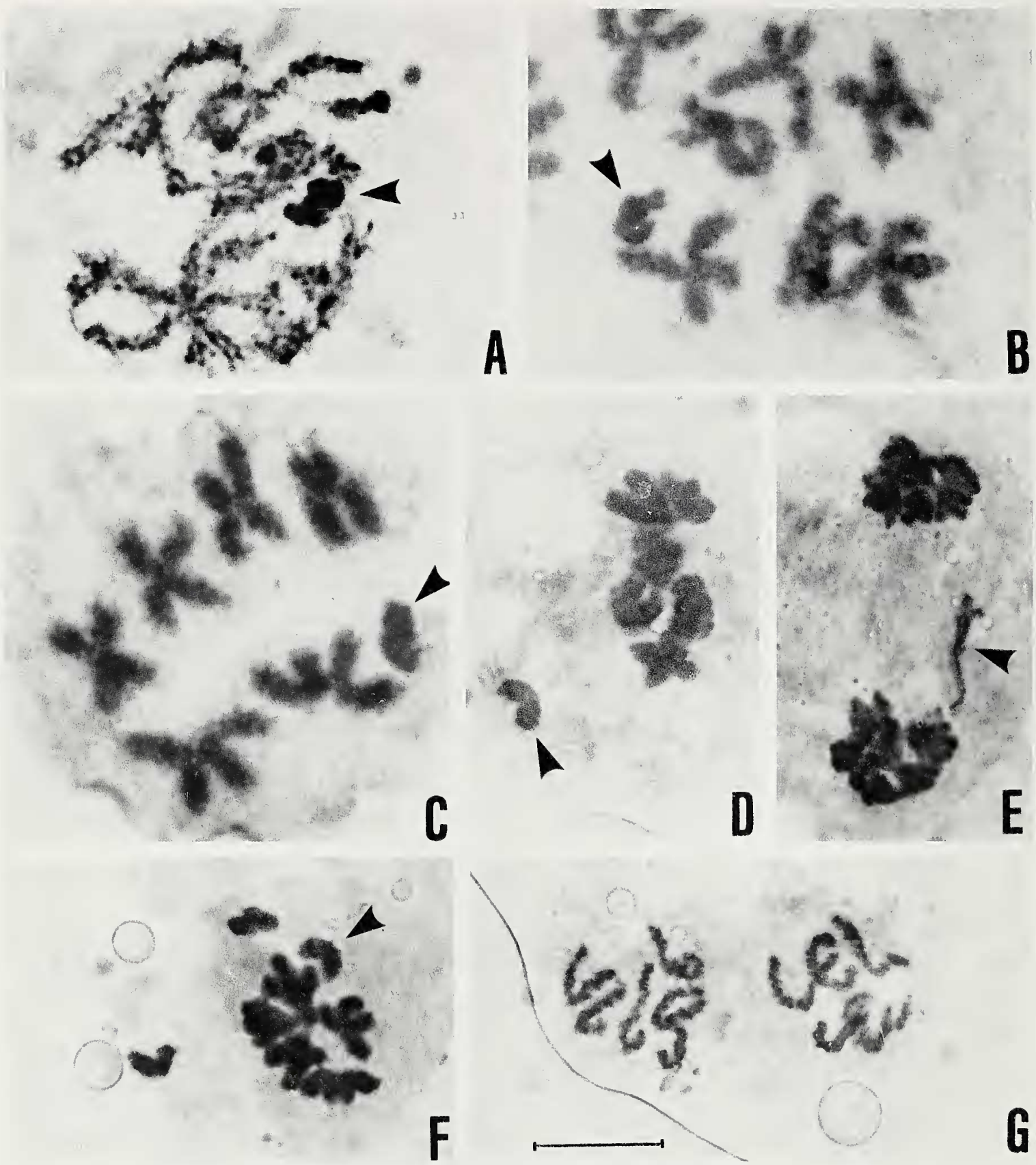

Figure 4.—*Scytodes globula* (2n = 13, n = 6 + X0). A) Early diplotene. B-C) Diakinesis. D) Metaphase I. E) Telophase I. F) Metaphase II; one chromosome has already separated its chromatids. G) Telophase II without X chromosome. Scale = 10 μm. Arrowheads point to the X chromosome.

alyzed there are marked differences in the cycle and degree of chromatin condensation during meiosis I, although during meiosis II the chromosome morphology is in accordance with that usually observed in spiders. More studies on chromatin organization and coiling are necessary in order to explain this uncommon behaviour.

The number and position of chiasmata, and even its absence, are under genetic control (Appels et al. 1998). Most organisms present a random chiasma distribution, and the number of chiasmata is related to the chromosome length, among other characteristics. In some species, an extreme chiasma localization in distal regions, and less frequently in proximal ones, has been described (John 1990). In insects, proximal chiasma localization has been described in Orthoptera with telocentric chromosomes (John 1990), and *S. globula* is an

example of proximal chiasma localization in metacentric chromosomes. Chiasma localization has genetic consequences since it leads to the appearance of large linkage groups, which are inherited as a unit, constraining the occurrence of recombination and hence, the generation of genetic variability.

Cytogenetic data in Dysderidae, Segestriidae, Filistatidae and Scytodidae are heterogeneous in many respects: kinetic activity (monocentric or holokinetic chromosomes); chromosome number, size and morphology; sex chromosome determining system; type of division of the sex chromosomes (pre- or post-reductional), and chiasma frequency and distribution. This cytogenetic heterogeneity raises many questions about the meiotic system and karyotype evolution within Haplogynae, and a more exhaustive study in other species of basal araneomorph spiders and even mygalomorph groups is necessary in order to explain the diversity encountered. This work is a first approach to the cytogenetic characterization of this spiders group. Further cytogenetic data together with morphological ones will contribute to a better understanding of the phylogenetic relationships in haplogyne spiders.

ACKNOWLEDGMENTS

This work has been supported by grants from Universidad de Buenos Aires (UBA) (TW01 to Drs. L. Poggio and L. Mola, and TX24 to Dr. J. C. Giacchi), from Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) (PIP 4217) to Dr. L. Poggio, and from Fundación Antorchas to Dr. A. Papeschi. The authors thank Lic. Pablo Rebagliati for collecting some specimens and María Constanza Pautasso for labeling and conditioning voucher specimens.

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Manuscript received 1 February 2001, revised 22 May 2001.